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REVIEW OF THE NORTH AMERICAN SPECIES OF *APOCRYPHA* ESCHSCHOLTZ, WITH A DESCRIPTION OF THE IMMATURE STAGES OF *APOCRYPHA ANTHICOIDES* (COLEOPTERA: TENEBRIONIDAE)

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The genus *Apocrypha* was established by Eschscholtz (1831) for *A. anthicoides* Eschscholtz. Subsequently *A. dyschirioides* was described from southern California by LeConte (1851) and *A. clivinoides* from the Owens Valley, California by Horn (1870). Recently 5 additional species have been described from Argentina (Kulzer, 1962; Kaszab, 1969). Lacordaire (1859) placed *Compsomorphus* Solier (1851) in synonymy under *Apocrypha,* and recognized the distinction of the genus by establishing the tribe Apocryphini, which has been recognized ever since. Gebien (1942) listed 6 genera under Apocryphini, including *Melytra* Pascoe from Tasmania and *Diplocyrtus* Quedenfeldt from Morocco. However, knowledge of these uncommonly collected beetles has grown by haphazard accretion, and the tribe will probably require redefinition when adequate material can be compared. The purpose of this paper is to review the species of *Apocrypha* occurring in North America and to describe the immature stages of *A. anthicoides* so that the information will be available for an analysis of the higher classification of Tenebrionidae (Doyen and Lawrence, 1979).

Materials and Methods

For morphological comparison adults and larvae were partially dissected, cleared in hot KOH and then completely dissected under binocular microscopes. Mouthparts and other sclerotized structures were mounted in glycerine jelly so that they could be viewed from various perspectives. Defensive glands and internal parts of the female reproductive tract were cleared, stained with chlorazol black and mounted in Canada balsam. Larvae were obtained by confining adults in containers half-filled with slightly moist sand and providing a variety of grains, dry dog foods and dead insects as food. Prepupal larvae were removed to petri dishes with a shallow layer of sand for pupation.

Apocrypha Eschscholtz

Apocrypha Eschscholtz, 1831:13; LeConte, 1851:137; LeConte, 1862:219;

Lacordaire, 1859:433; Horn, 1871:390; LeConte and Horn, 1883:384; Kulzer, 1962:98; Kaszab, 1969:328.

Compsomorphus Solier, 1851:206; Lacordaire, 1859:433 (synonymy). Type species: *Compsomorphus elegans* Solier (monobasic).

Very small beetles with globular prothorax, constricted, petiolate mesothorax and long slender legs with clavate femora. Eyes moderate, nearly round or with slight anterior emargination; antennae slender, filiform basally, becoming slightly clavate and serrate apically; labrum transversely subrectilinear with medial processes of tormae transverse; mandibles elongate, with prominent retinaculum and smooth (nonstriate) mola; maxillae with galea densely setose, lacinia with 2 large apical teeth and subapical brush of stout setae; labrum small, exposing ligula and maxillae; tentorium with sides short, straight, reaching occipital foramen; tentorial bridge straight (not arched), situated posteriorly. Prothorax globular, rounded, without defined angles or lateral carinae; procoxal cavities closed externally and internally. Mesocoxal cavities closed laterally by apposed sterna, trochantin concealed; mesendosternite with short, slender dorsal arms and stout, horizontal, apically enlarged anterior arms; elytra oval, inflated, abruptly constricted basally; epipleuron narrow, extending from humerus to elytral apex. Metanotum membranous; metendosternite with short, broad stalk, long stout arms without laminae extending to vicinity of elytral articulations and terminating in large apical flanges; tendons inserted medially; wings absent. Abdomen with external membranes between segments 3–5; abdominal glands small, saccate, without annulations; ovipositor with gonostyles small, subapical; aedeagus with tegmen dorsal.

Type species: *Apocrypha anthicoides* Eschscholtz (monobasic).

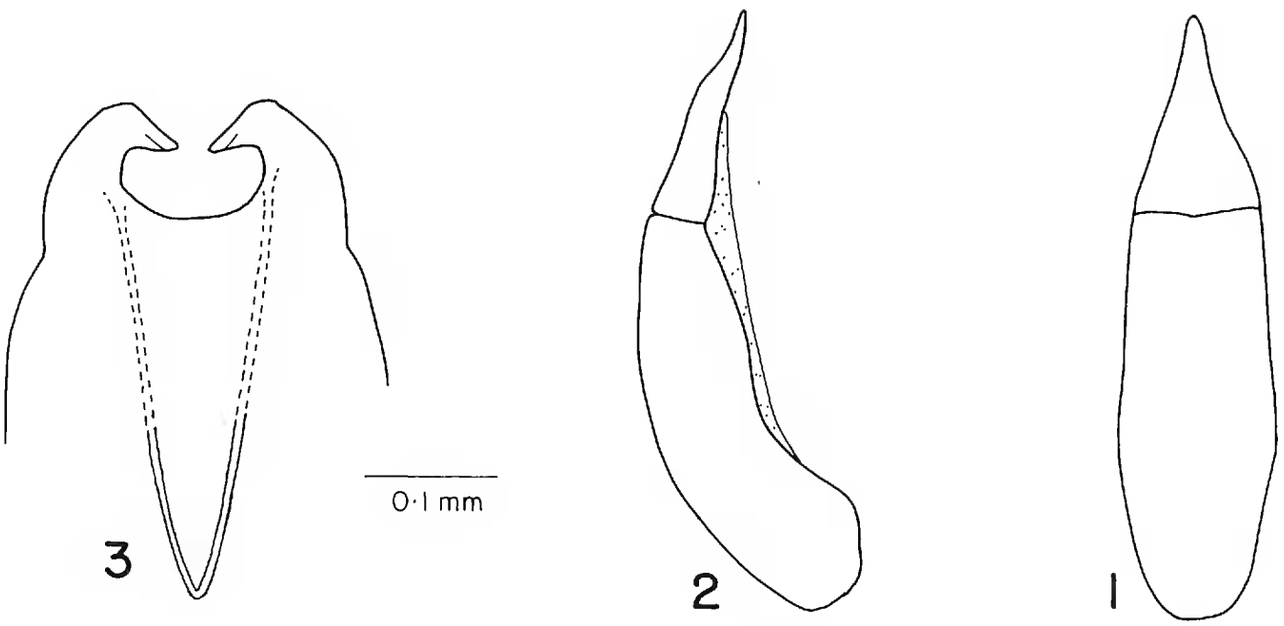
The North American species of *Apocrypha* can be separated by the following key.

1. Pronotum with 2–8 long, projecting setae near each lateral margin of disk; antennae with 3rd segment about 1.3 times longer than 4th . . . 2
   Pronotum without long, projecting setae; antennae with 3rd segment subequal to 4th ..... *anthicoides*
2. Pronotum with 2 long projecting setae near each lateral border of disk; elytra without long, projecting setae ..... *clivinoides*
   Pronotum with 4–8 long projecting setae near each lateral margin of disk; elytra with scattered long setae projecting from disk, denser on humeri and declivity ..... *setosa* n.sp.

Apocrypha anthicoides Eschscholtz
(Figs. 1–3)

Apocrypha anthicoides Eschscholtz, 1831:13.

Apocrypha dyschirioides LeConte, 1851:137. **NEW SYNONYMY.**



Figs. 1–3. *Apocrypha anthicoides*, male genitalic structures. Figs. 1–2, aedeagus, dorsal and lateral, respectively. Fig. 3, eighth sternite and spiculum.

This common species is easily recognized by the 3 rows of about 6 long, erect setae on each elytron; by the absence of long, erect setae on the pronotum; by the barely emarginate eyes; and by the polished lustrous cuticle. The head, pronotum, elytra and abdominal sternites are relatively sparsely punctate, with the punctures separated by about 1.5–2 puncture diameters. The first 3 abdominal sternites are clearly connate, without incised intersegmental sutures. The 8th sternite of the male is deeply emarginate (Fig. 3), and the aedeagus abruptly attenuate to an acutely rounded, upturned apex (Figs. 1–2).

The characters cited by LeConte (1851) and Horn (1870) as distinguishing *A. anthicoides* from *dyschirioides* involved differences in punctation, body size and color. Color ranges from pale tan (in obviously teneral individuals) through brown to black or dark brown with paler elytral humeri. Body length (measured as elytral length plus pronotal length) varies from 1.9–3.1 mm. The smallest individuals are dark brown to black and are predominantly from localities near the seacoast. Larger, brownish individuals and those with pale humeri are predominantly from interior localities. There is continuous variation in both color and size, and large collections from many localities include a range of phenotypes. This pattern of variation appears to conform to Gloger's ecogeographic rule, which has been applied to various other insects (Mayr, 1963:324).

Horn (1870) stated that the pronotum was longer than broad in *A. dyschiriodes*, broader than long in *anthicoides*. Measurement of numerous individuals showed that the pronotum is always broader than long, with continuous variation in both dimensions. Furthermore, the distinctive male

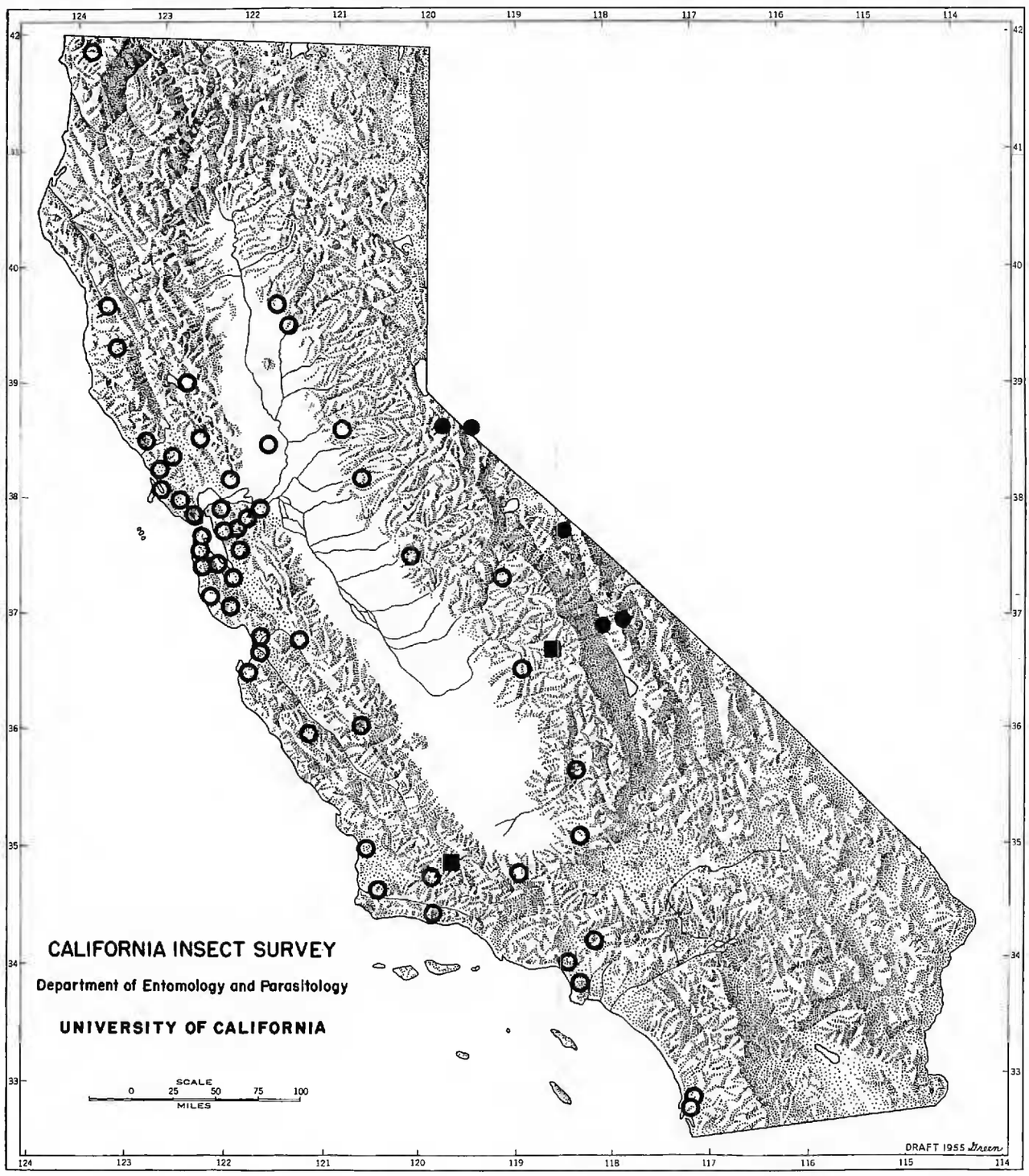
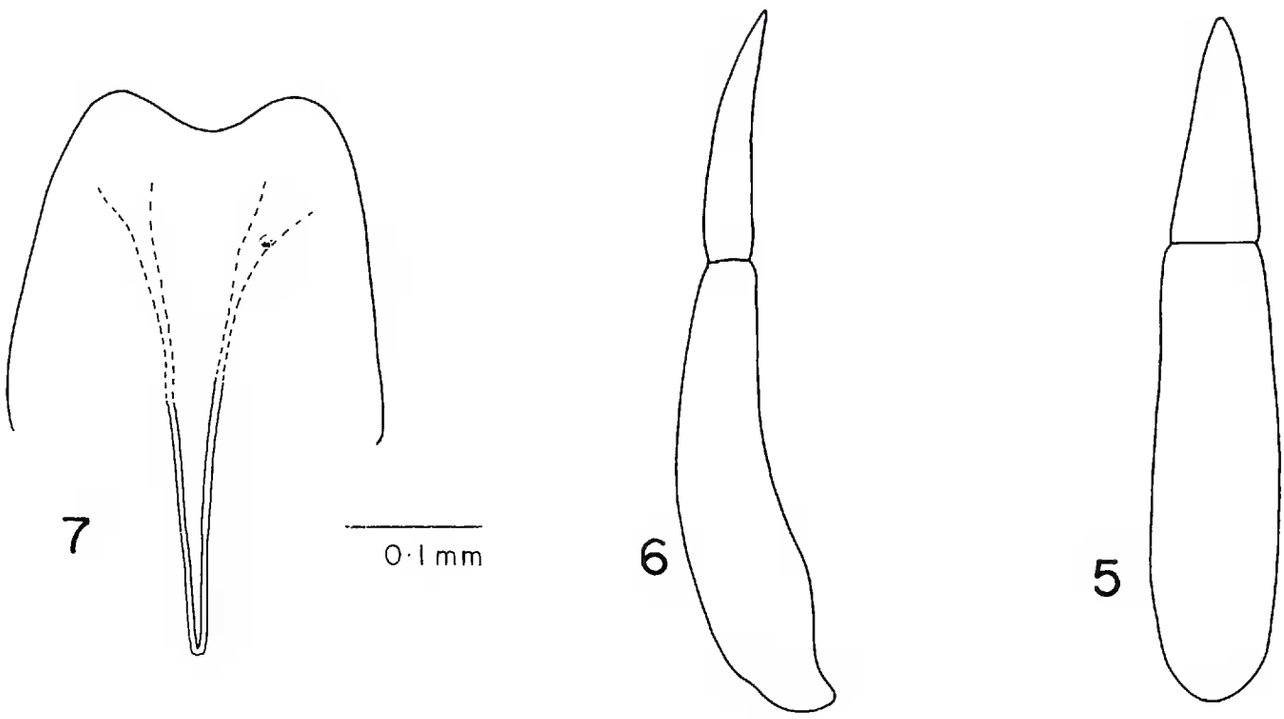


Fig. 4. Distribution of *Apocrypha anthicoides* (open circles), *A. clivinoides* (closed circles) and *A. setosa* (squares).

genitalic characters (Figs. 1–3) were exhibited by all individuals, indicating that a single species is represented.

Apocrypha anthicoides is common below 1200 m from northern Mendocino County and Butte County, south through the Sierra Nevada and the coast ranges to San Diego County (Fig. 4). *A. anthicoides* occurs in coastal sage scrub, chaparral, and about the margins of salt marshes in the coastal part of its range. Interior populations inhabit deciduous or mixed deciduous-



Figs. 5–7. *Apocrypha clivinoides*, male genitalic structures. Figs. 5–6, aedeagus, dorsal and lateral views, respectively. Fig. 7, eighth sternite and spiculum.

coniferous woodland or chaparral habitats, especially in relatively well-drained situations. Nearly all individuals are collected by Berlese extraction of leaf or needle litter.

Apocrypha clivinoides Horn

Apocrypha clivinoides Horn, 1870:391.

The more depressed, elongate form and slightly larger size clearly distinguish this species from *anthicoides*. It is similar to *setosa,* but slightly smaller and has only 2 pairs of long projecting setae on the pronotum (4–8 pairs in *setosa*).

The elytra are densely covered by pale, appressed setae, but lack long, erect setae. The eyes are slightly emarginate, and the cuticle is very finely granulate and dull. The head, pronotum and elytra are densely, almost confluently punctate. The anterior 3 abdominal sternites are separated by incised intersegmental sutures, and the 8th sternite of the male is longer than broad and shallowly emarginate (Fig. 7). The aedeagus gradually attenuates to a sharply rounded apex which is not upturned (Figs. 5–6).

Material examined (Fig. 4).—Calif., Alpine Co., 1 mi. E Woodfords, X-30-1965, N. Ueshima, ex litter *Artemsia* (9); Fresno Co., Summit Meadow, VI-4-1911, R. Hopping (1); Inyo Co., Goodale Creek, N. Lone Pine, IV-3-1953, R. E. Leech (1); 7 mi. SE Benton Crossing, VI-15-1970, M. S. Was-

bauer and F. G. Andrews (1); Waucoba Spr., IV-30-1975, ex litter *Pinus monophylla,* F. G. Andrews (1); Nev., Douglas Co., Topaz Jct., VII-19-1975, ex litter *Pinus monophylla,* A. R. Hardy, F. G. Andrews (3). The single specimen from Summit Meadow, Fresno County, is the only record from west of the Sierran crest. Since the place name Summit Meadow occurs 3 times in Fresno County, an exact collection locality cannot be specified.

Apocrypha setosa, new species
(Fig. 8)

Body slender, elongate, slightly depressed dorsoventrally, medium brown to nearly black; cuticle finely granulate, weakly shining or dull. Head subhexagonal in dorsal aspect, anterior epistomal margin straight; eyes with anterior margin straight or slightly emarginate; ommatidia coarse, numbering about 30 per eye, and set with fine setae at intersections; vertex, frons, genae and subgenae closely, almost confluently set with punctures about as large as ommatidia, and densely clothed with long, pale, appressed setae directed anterad; longer, erect setae located as follows: 1–3 dorsad of each eye, 1–4 in irregular submedian row on each side of vertex and frons, 1–3 near anterolateral corners of epistoma.

Pronotum with broadly rounded anterior corners, sides nearly parallel in anterior half, strongly, evenly converging in posterior half; disk slightly flattened, closely, nearly confluently set with punctures about as large as ommatidia, and densely clothed with pale, appressed setae directed posterad; each lateral margin set with 4–8 long setae projecting dorsolaterally; hypomera and sternum coarsely punctate to punctatorugose, with setal clothing less dense than on disk; sternum bearing about 10–15 long, erect setae. Elytra irregularly set with punctures slightly larger than those on prothorax, separated by about 1–2 puncture diameters, and bearing pale, posteriorly declined setae producing a sparser clothing than on thorax; long, erect setae located as follows: 3–10 in each humeral region; 2–8 arranged in 2 irregular rows on each side of disk; about 25 in irregular patch on declivity. Thoracic and abdominal sternites closely, almost confluently punctate to punctatorugose, and densely set with long, pale, appressed setae interspersed with occasional erect setae; intersegmental sutures incised. Femora, tibiae and tarsi densely covered with pale, appressed setae. Aedeagus gradually attenuate to sharply rounded apex (as in Figs. 5–6); eighth sternite shallowly emarginate (as in Fig. 7).

Length (pronotum plus elytra), 3.0–3.3 mm.

Holotype female and 12 paratypes from New Cuyama, Santa Barbara Co., Calif., VI-28-1975, ex litter *Quercus wizlizenii,* Hobza and Muldowney, colls.; 1 paratype from S. Fork Kings River Canyon, 5000′, Fresno Co., Calif., VII-4-1910. The holotype and one paratype are deposited in the Cal-

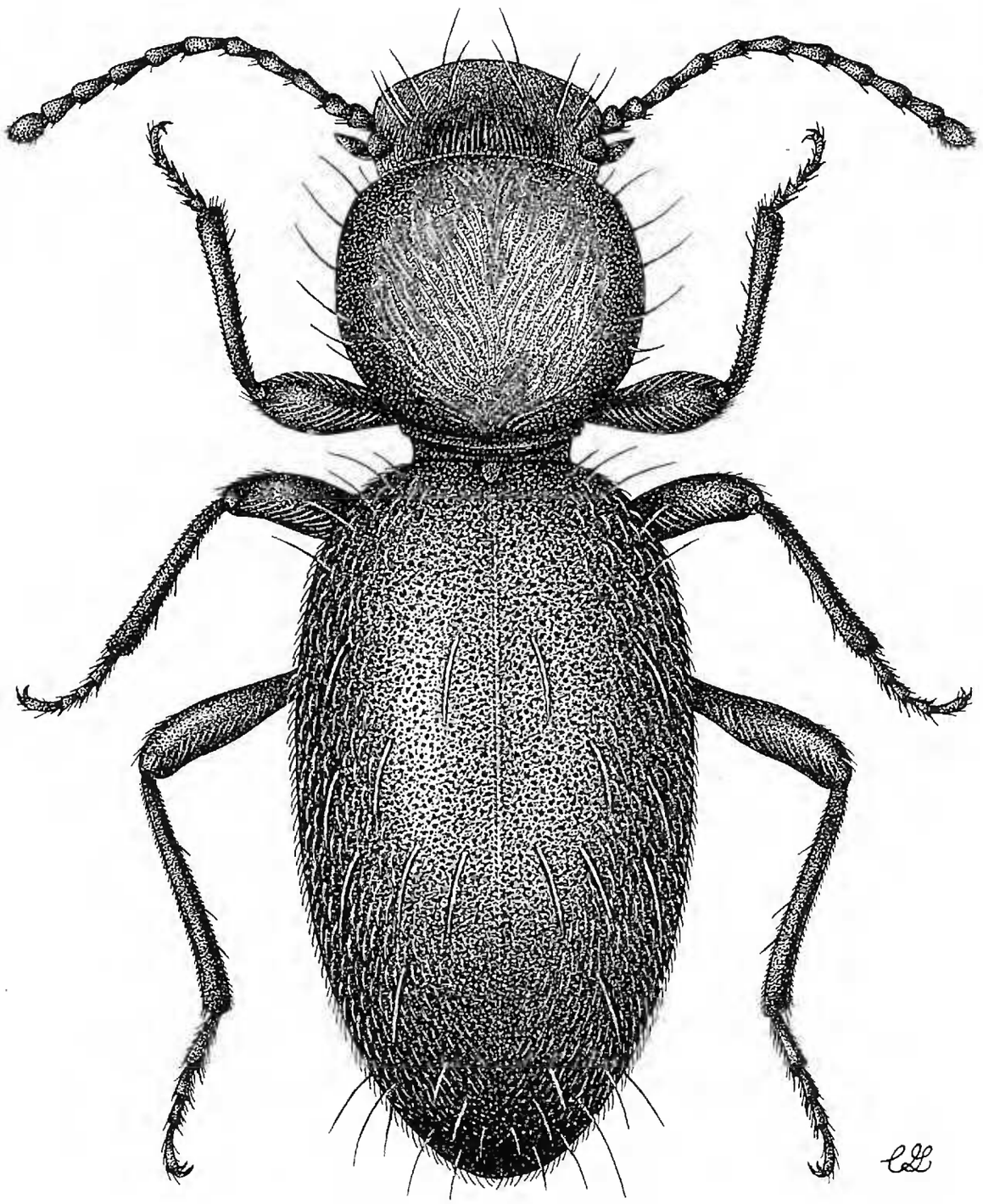


Fig. 8. *Apocrypha setosa,* dorsal aspect.

ifornia Academy of Sciences, San Francisco and paratypes in the collection of the California Department of Food and Agriculture, Sacramento and the Essig Museum of Entomology, Berkeley, California.

The long setae projecting from the lateral margins of the pronotum distinguish *A. setosa* from *anthicoides,* which lacks long setae on the thorax. The larger number of long pronotal setae and the long, erect setae on the elytra of *setosa* distinguish it from *clivinoides,* which averages about 20 percent smaller. Counts of setae vary, even between sides of a single spec-

imen. This variation is partly traumatic, and stubs of setae may be found on some specimens.

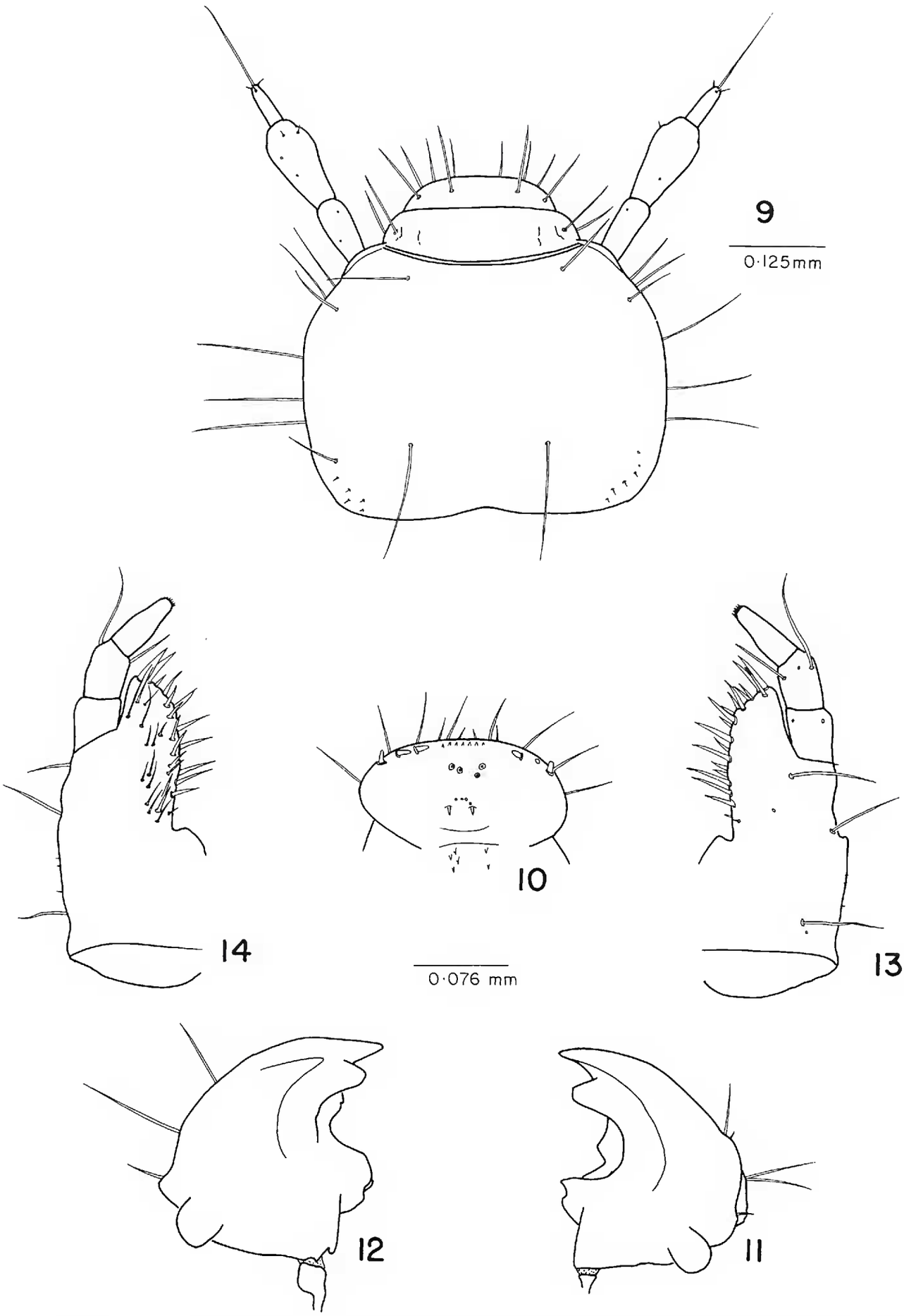
A. setosa and *clivinoides* appear to be largely allopatric, but each is known from a single individual from Fresno County. Unfortunately, as mentioned above, the exact collection locality for *clivinoides* cannot be determined.

Description of the Immature Stages of *A. anthicoides*

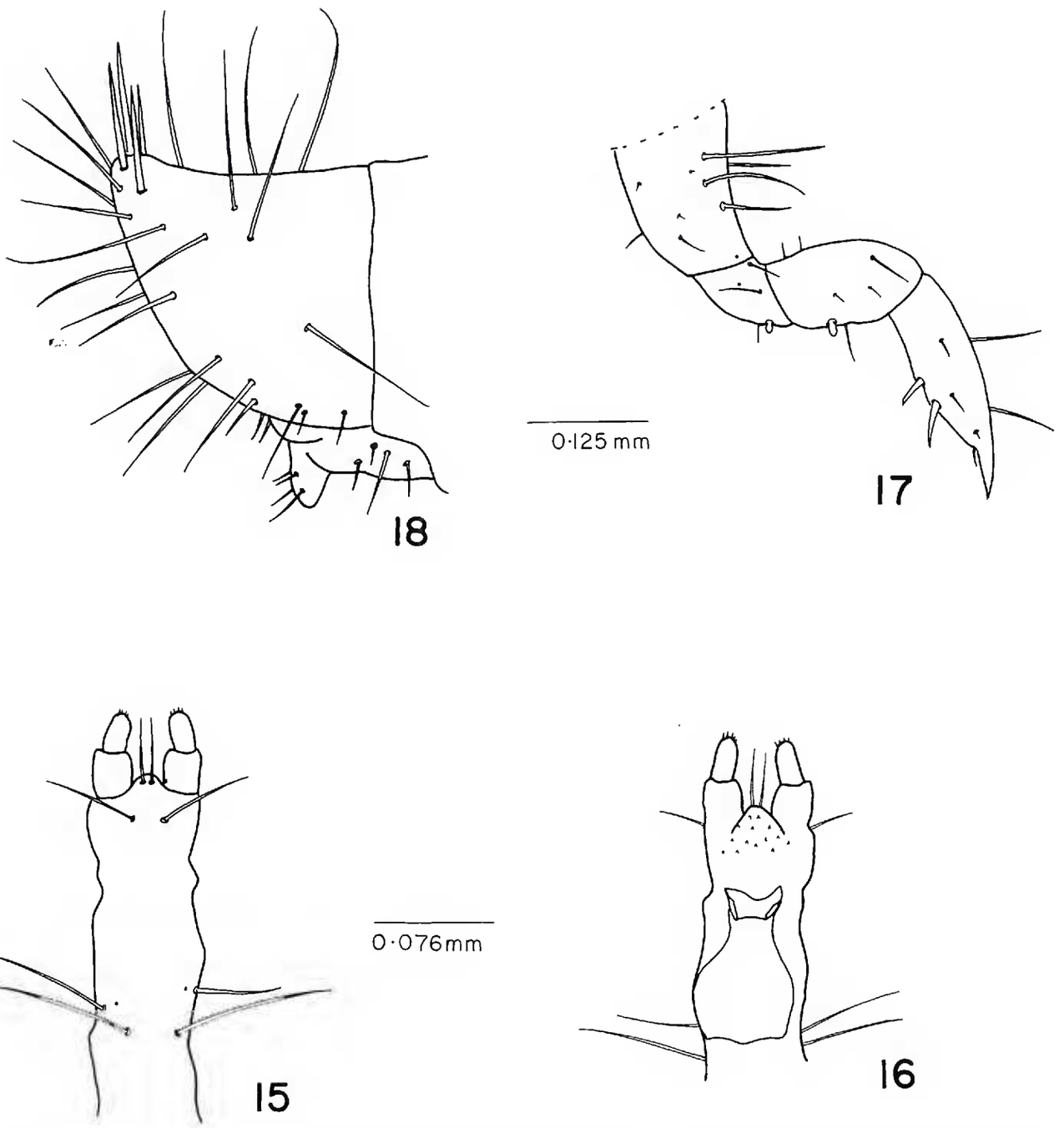
Mature larva (Figs. 9–18).—Body elongate, cylindrical, pale tan in alcohol preserved specimens, creamy in life; cranium, thorax, legs and abdomen lightly sclerotized, fragile; maxillae, clypeus, labrum and labium moderately sclerotized, tan; mandibles and claws heavily sclerotized, dark brown to black.

Cranium (Fig. 9) subquadrate with rounded corners; prognathous, without ocellar lenses; cuticle finely rugose with few setae scattered dorsally and laterally and few short spines posterolaterally; labrum evenly arcuate, with 10 long setae dorsally and marginally; epipharynx (Fig. 10) with 6 short, blunt setae marginally, scattered circular sensillae centrally, and 2 short spines basally; antennae articulated on prominences just laterad of clypeus (Fig. 9); basal segment cylindrical, slender; 2nd segment clavate; 3rd segment shorter, slender, with 1 long and several shorter setae at apex; mandibles (Figs. 11–12) stout with strongly bidentate incisor lobe and massive mola with multituberculate anterior prominence; retinaculum prominent, midway between mola and incisor teeth; basolateral corner of mandible bearing several long, coarse setae; maxillae (Figs. 13–14) with cardo triangularly arcuate, poorly differentiated from stipes; mala with row of stout, sharp setae on medial margin and irregularly scattered finer setae medially on dorsal surface; maxillary palp with basal 2 segments subequal, bearing 2 long setae or setal sockets; apical segment about 1.3 times length of 2nd, gradually narrowing to rounded apex bearing minute, spine-shaped sensillae; labium (Fig. 15) elongate, with submentum, mentum and prementum not delimited by sutures; bearing 4 long setae basally, 2 apically and 2 anteriorly directed shorter setae on ligula; palp with segments subequal in length; apical segment finer, bearing minute, spine-shaped sensillae apically; hypopharynx (Fig. 16) with low, symmetrical, anteriorly concave sclerome; dorsal surface of ligula bearing about 15 sharp teeth.

Prothorax nearly as long as 1st abdominal segment, flattened, partly enveloping head in contracted specimens, glabrous at 100× magnification except for few scattered long projecting setae dorsolaterally and laterally; mesothorax and metathorax similar, about ⅔ length of 1st abdominal segment; sterna transverse, postcoxales separate on all segments. Legs similar, but prothoracic pair (Fig. 17) about 1.3 times larger than posterior pairs; lightly sclerotized except for articulations, with sparse, scattered setae; cox-



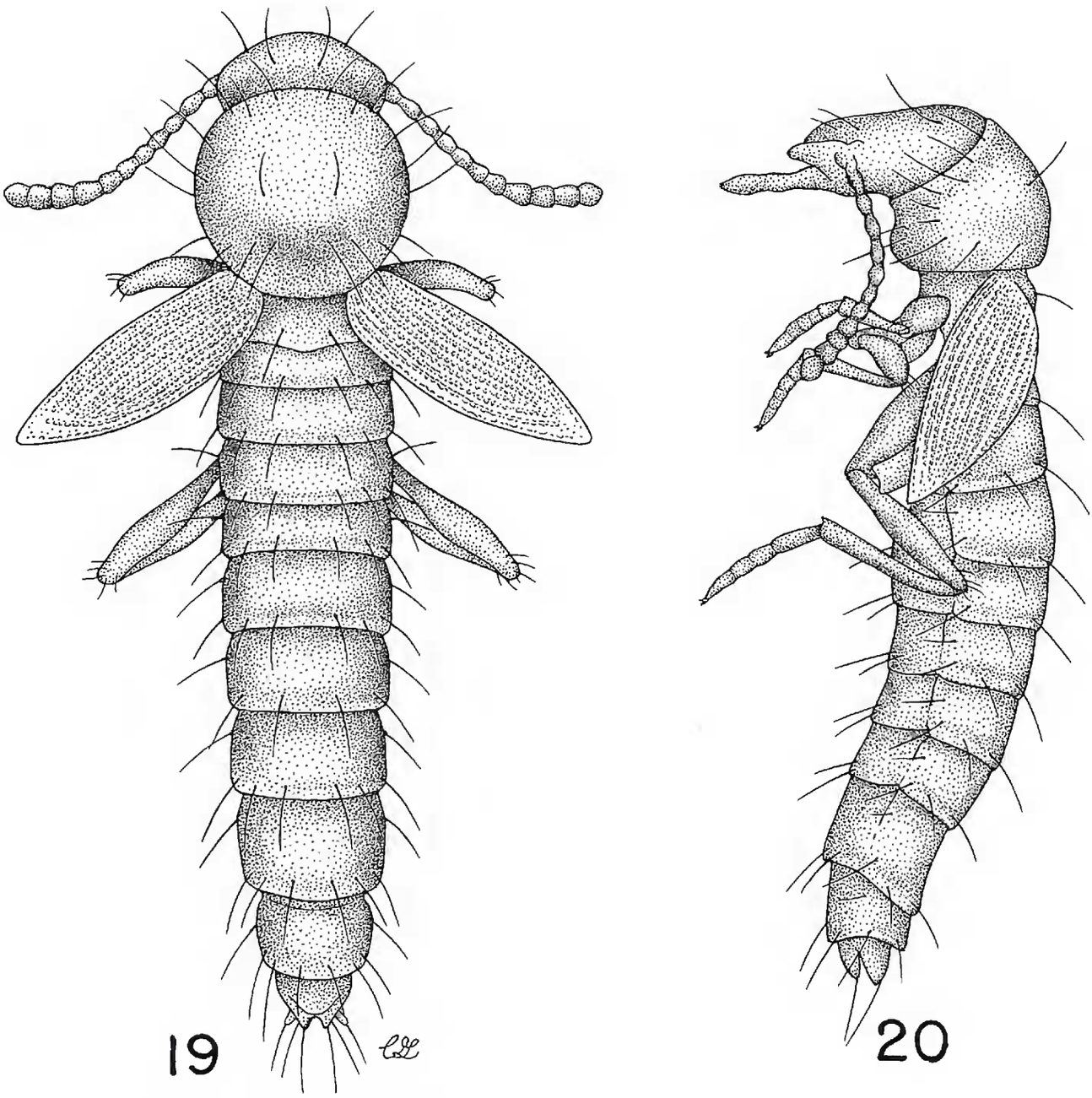
Figs. 9–14. *Apocrypha anthicoides*, larval structures. Fig. 9, dorsal aspect of head. Fig. 10, epipharynx. Figs. 11–12, dorsal aspect of right and left mandibles. Figs. 13–14, ventral and dorsal aspects of left maxilla.



Figs. 15–18. *Apocrypha anthicoides*, larval structures. Fig. 15, labium. Fig. 16, hypopharynx. Fig. 17, anterior aspect of left foreleg. Fig. 18, lateral aspect of abdominal apex.

ae directed anteroventrally, forecoxae contiguous, middle and hind coxae separated by about 1.5 coxal diameters; trochanters short, triangular, with single tuberculate seta on each foremember, slender setae on posterior pairs; femora about as long as coxae, stout, bearing single tuberculate seta on each foremember; tibiae subequal in length to femora, broadest in middle and bearing 2 large, stout setae on mesal surface of each foremember, slender setae on posterior pairs; claw stout, sharp, without differentiated base and apex.

Abdominal segments cylindrical; segments 1–8 subequal, subquadrate in



Figs. 19–20. *Apocrypha anthicoides,* pupa, dorsal and lateral aspects respectively.

dorsal aspect, glabrous at 100× magnification except for sparsely scattered long setae dorsolaterally and laterally; 9th segment (Fig. 18) about half length of preceding segments, tapering to rounded apex bearing 4 stout, stiff, erect spines and bearing numerous long slender setae on dorsal, lateral and ventrolateral surfaces; 10th segment small, subtending 9th, with short, blunt pygopods posteriorly. Spiracles simple, annular.

Length, 5.5–6.5 mm; head capsule width, 0.49–0.52 mm.

Pupa (Figs. 19–20).—Elongate, subcylindrical with enlarged globular prothorax, diagonally projecting elytra, and deflexed head; cream colored with long fine setae.

Head elongate, slightly depressed, exserted and deflexed beneath pro-

thorax (Fig. 19); vertex and epistoma with sparsely scattered, long, erect setae; antennae free, extending posterolaterally above or below forelegs and elytra.

Prothorax globular, excavated anteroventrally for reception of head; lateral margins rounded, without trace of carina; pronotum nearly round in dorsal aspect, with scattered, long, erect setae peripherally; mesonotum about ⅓ as long as pronotum, narrower anteriorly, subequal in width to metanotum posteriorly, and bearing 2 long setae between elytra; elytra directed diagonally backward and slightly downward or nearly horizontal, faintly 9-striate, glabrous; metanotum short, transverse, bearing 2 long erect setae; wing sheaths about ¾ as long as elytra, without apparent venation; metacoxae projecting ventrally well below level of abdomen. Femora clavate, with short setae on knees.

Abdominal segments 1–6 subcylindrical, about twice as broad as long, bearing sparsely scattered, long, posteriorly declined setae; lateral margins without gin traps, but with 2 small tubercles each bearing long, projecting seta; segment 7 tapering, rounded posteriorly; abdominal apex with apparently 2-segmented projecting papillae in female, shorter unsegmented papillae in male.

Length, 3.0–3.5 mm.

Material examined.—5 larvae, laboratory reared from adults collected in Calif., S. L. Obispo Co., San Simeon, IV-1976, C. Y. Kitayama; harvested XII-1976. 20 larvae, 6 pupae, laboratory reared from adults collected in California, S. L. Obispo Co., 3 mi. S Oceano, II-23-1975, J. Doyen; harvested IV-18 to VII-24-1975.

The larvae of *Apocrypha* are superficially very similar to larvae of *Tribolium* and other small Ulomini. As elaborated below, this similarity extends to several anatomical details. Berlese extraction yielded only adult beetles, suggesting that the larvae inhabit deeper layers of the soil. The absence of gin traps on pupae is unusual in Tenebrionidae. Presumably the tiny lateral abdominal tubercles represent reduced gin traps. Presence of pupal wing sheaths in brachypterous or flightless Coleoptera is common (Smith, 1964; Spilman, 1979). In species in which the adult is entirely wingless, the pupal wing sheath is usually much shorter than the elytral sheath, and the adult wing is absent or only partly fills the sheath, and degenerates before the adult emerges. *Apocrypha* is unusual in that the adult is completely apterous with the metanotum reduced to a membrane, yet the pupal wing sheaths are about two-thirds as long as the elytral sheaths and about half as broad. No imaginal wings are visible within the pupal sheaths, although wings could have been present and degenerated, since the ages of the pupae are unknown.

Spilman (1979) examined pupae of various wingless and brachypterous Coleoptera, and concluded that in general pupal wing sheaths are short or

absent in taxa in which brachyptery or winglessness is widespread. In contrast, in taxa with occasional wingless or brachypterous members, pupal wing sheaths are long. This might suggest that *Apocrypha* represents a specialized, wingless member of some larger taxon containing mostly winged species. However, the apparent total absence of imaginal wings suggests derivation from a higher taxon in which wing reduction is widespread. The only other species of Apocryphini which we have dissected, *A. clivinoides,* is apterous.

Apocrypha shows some other interesting differences between the pupa and adult. In the adults long, erect setae are present on the elytra and head, absent from the thorax. In the pupa, setae are present on the head and pronotum but absent on the elytra. The elytra of adult *Apocrypha anthicoides* are without defined striae, although striae are present in some South American species (Kaszab, 1969). In pupae of *A. anthicoides* striae are visible, though very faint in some specimens. These pupal striae are difficult to count, but apparently are nine in number.

Phylogenetic Relationships

Apocryphini has been placed as a tribe in the subfamily Tenebrioninae since the work of Lacordaire (1859), who suggested a position close to Helopini. Watt (1974) treated Apocryphini as a tribe of Lagriinae, but indicated only a few characters of adults which support this relationship—notably, the absence of lateral pronotal carinae (shared with Lagriini) and the presence of 10-striate elytra in some (unspecified) species (universal in Lagriinae). Similarities resulting from loss of structures (such as carinae) can easily arise through convergence. The retention of 10 elytral striae is a primitive feature in Coleoptera, and not very useful in indicating cladistic relationship. Moreover, the pupal elytra of *A. anthicoides* bear only 9 striae, suggesting that this may be the primitive number for the genus.

Watt's Lagriinae is defined primarily by characters of the larvae, especially the structure and position of the antennae. In most Tenebrionidae the larval antennae have three subequal segments or have the third segment variably reduced. In Lagriinae the larval antennae have two densely pubescent segments, with the second much longer than the first. The second segment bears a distinctive sensorium or group of sensillae at the apex, and the antennae are clearly separated from the bases of the mandibles by a strip of cuticle (contiguous in all other Tenebrionidae except Nilionini). In addition the epipharynx and hypopharyngeal sclerome are highly asymmetrical in Lagriinae (symmetrical in most Tenebrionidae). In all of these features *Apocrypha* exhibits the generalized character state common to Tenebrioninae and most other subfamilies. In addition, the larva of *Apocrypha* is elongate, cylindrical, and weakly sclerotized. Larvae of Lagriinae are

usually much stouter, flattened and moderately sclerotized, especially dorsally.

Several features of adult *Apocrypha* indicate derivation from Tenebrioninae. The labrum is short and transverse (elongate in Lagriinae) and the epipharynx membranous and symmetrical (asymmetrical with sclerotized plates in Lagriinae). The ovipositor has the gonostyles short and situated subapically. In Lagriinae, Diaperinae and most other primitive subfamilies the gonostyles are elongate and apical. The defensive glands are small and saccate, and the bursa copulatrix bears a single accessory tube which branches to form the spermatheca and the accessory gland. Diverse glandular structures occur in Lagriinae, but simple saccate glands without extrinsic musculature are not represented (Tschinkel and Doyen, in press). In many Lagriinae multiple spermathecal tubules originate independently from the bursa. In other Lagriinae the bursa (which may be constricted to produce 2 subequal chambers) bears a single, unbranched tube which apparently represents the spermathecal accessory gland.

Precise affinities of Apocryphini within Tenebrioninae cannot be specified with certainty. Lacordaire's Helopides contained Adeliini, Misolampini and Helopini, as well as *Apocrypha*. These taxa share only a general similarity in superficial external characters, and are now classified in remote parts of the Tenebrionidae. Misolampini appear synonymous with Coelometopini based on structures of defensive glands and the female reproductive tract (Tschinkel and Doyen, in press), which are very different than those in *Apocrypha*. Described larvae of Helopini have long, recurved urogomphi, frequently opposing sclerotized processes on abdominal tergite eight, and have the hypopharyngeal sclerome tridentate apically. The larva of *Apocrypha* lacks urogomphi, has the sclerome concave anteriorly and the head and mouthparts differ in many structural details from those of Helopini (see Byzova and Gilyarov, 1956).

Several of the larval features of *Apocrypha* are shared with Opatrini and/or the *Tribolium* group of Ulomini. For example, the third antennal segment is relatively large in *Tribolium, Palorus* and *Alphitophagus* (Ulomini), as in *Apocrypha*. The mandibles of *Apocrypha,* with large, subequal incisor teeth and the large anterior molar prominence, are similar to those of many Ulomini and Opatrini (see Hayashi, 1966). Likewise, the anteriorly concave hypopharyngeal sclerome is shared with many representatives of those tribes. The enlarged forelegs of *Apocrypha,* with modified, peg-shaped setae on the trochanter and femur, are similar to those of many Opatrini and Pedinini (see Hayashi, 1966; Keleinikova, 1966; Skopin, 1960). Finally, the stiff marginal spines on the apex of the ninth abdominal tergite are shared with many Opatrini and Ulomini.

Some of the features discussed above are probably plesiomorphic and not indicative of cladistic relationships. For example, the relatively elongate

antennae, with approximately equal segments, are probably primitive to the subfamily Tenebrioninae, if not the entire family. Other features, such as the enlarged forelegs with specialized spination, and the elongate, cylindrical body without urogomphi are shared by soil inhabiting species from several tribes (e.g., the *Pedobionta* of Skopin, 1964 or the combined tenebrioid and opatroid lineages of Keleinikova, 1963). Such features may have arisen convergently in *Apocrypha*. However, the balance of characters indicates a position near Opatrini or Ulomini, where Apocryphini should be retained as a separate tribe until its relationships can be further elucidated.

Acknowledgments

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